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The early visual encoding of a face (N170) is viewpoint-dependent: A parametric ERP-adaptation study

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ABSTRACT

Visual representations of faces are extracted shortly after 100 ms in the human brain, leading to an occipito-temporal cortex N170 event-related potential (ERP). To understand the nature of this early visual representation, a full-front adapting face preceded a different or identical target face identity. The target face varied parametrically in head orientation from the adapting face (0–90°, 15° steps). The N170 elicited by the target face increased progressively from 0° up to 30° head orientation, with no further increase until 90°. The N170 decreased for repeated face identities, this effect being stable between 0° and 30° changes of viewpoint, and no effect beyond that angle. These observations suggest that a face is encoded in a view-dependent manner, being matched to either a full-front or a profile face view. Yet, individual face representations activated as early as the peak of the N170 generalize partially across views.

1. Introduction

The human brain is able to recognize individual faces across different head orientations in depth, a particularly challenging task (Burton, Bruce, & Hancock, 1999; Hancock, Bruce, & Burton, 2000). However, the nature of the operations underlying this performance, which is known to be improved by long-term familiarity with the faces (Young, Hay, McWeeny, Flude, & Ellis, 1985), remains unknown. Traditional models of face recognition postulate that an initial stage of structural encoding is based on a view-dependent structural representation (Bruce & Young, 1986; Burton et al., 1999), which would possibly precede a stable, viewpoint-invariant representation, allowing for subsequent recognition of the face.

Regardless of face identity, single-cell recording studies in the non-human primate brain have shown that most face-selective cells in the monkey inferior temporal cortex (IT), in particular in the superior temporal sulcus (STS), are tuned to specific head orientations, showing a progressive reduction of the response with increases in angle disparity (Desimone, Albright, Gross, & Bruce, 1984; Perrett et al., 1985, 1991; for more recent evidence see Freiwald & Tsao, 2010). Neurons with viewpoint-invariance responses have also been reported in more anterior regions of the monkey IT (Freiwald & Tsao, 2010). In humans, behavioral studies using repetition paradigms, also called adaptation or priming paradigms, have suggested that face representations are viewpoint-dependent in the human visual system, namely that there are different representations for different head orientations (Benton, Jennings, & Chatting, 2006; Fang & He, 2005; Hill, Schyns, & Akamatsu, 1997; Jiang, Volker, & O'Toole, 2007; O'Toole, Edelman, & Bülthoff, 1998; Troje & Bülthoff, 1996). Most functional magnetic resonance imaging (fMRI) studies have also found release from adaptation for different head orientations of unfamiliar faces in face-selective areas of the occipito-temporal cortex (e.g., Andrews & Ewbank, 2004; Axelrod & Yovel, 2012; Fang, Murray, & He, 2007; Grill-Spector et al., 1999; also see Xu & Biederman, 2010).

Surprisingly, despite numerous scalp event-related potentials (ERPs) studies with face stimuli, whether the N170 (or the M170 in magnetoencephalography, MEG), a component peaking at around 170 ms over occipito-temporal regions (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996; Jeffreys, 1989 for earlier studies; Rossion & Jacques, 2011 for review), reflects viewpoint-independent responses, remains unknown. This N170 component is particularly interesting because it is a reliable marker of the earliest activation of a face representation in the human brain. That is, in contrast to less consistent earlier face-sensitive responses, for instance at the level of the

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P1, the larger N170 to faces is not accounted for by low-level visual cues (Rossion & Caharel, 2011) and the N170 is evoked by many different formats of faces (e.g., Sagiv & Bentin, 2001; for reviews Rossion, 2014; Rossion & Jacques, 2011). In order to understand further the nature of this early face representation, a number of relatively recent studies have used an ERP adaptation paradigm in which a face stimulus is preceded by a stimulus of another category, or a face stimulus under a different format (e.g., Eimer, Kiss, & Nicholas, 2010; Kovacs et al., 2006; Zimmer & Kovács, 2011). However, to our knowledge, no studies have compared the N170 response to a given head orientation preceded by a face under the same or a different head orientation. This is the first goal of the present ERP study, in which a full-front face served as an adapter for target face views that departed linearly from that adapter, from 0° until 90° of head rotation in depth.

Importantly, this issue should not be confused with the question of whether adaptation to the *identity* of a face is invariant to changes in head orientation. For instance, the N170 is reduced in amplitude in response to an immediately repeated individual face stimulus as compared to the response to an unrepeated face stimulus (e.g., Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Caharel, Jiang, Blanz, & Rossion, 2009; Harris & Nakayama, 2007; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Jacques, d'Arripe, & Rossion, 2007; Jacques & Rossion, 2009). The effect takes place on the peak of the N170, indicating that *individual* face representations are extracted as early as about 170 ms after stimulus onset in the occipito-temporal cortex (Rossion & Jacques, 2011). Repetition effects for individual unfamiliar faces have been also found despite substantial changes of viewpoint (30°) between the two faces presented successively (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2011; Caharel, Jiang, et al., 2009; also see Ewbank, Smith, Hancock, & Andrews, 2008). However, in these studies, there was always a change of head orientation (30°) between an adapter and a target face, which was of the same or of a different identity. Other ERP studies have used only one head view, or only small changes of head orientation (Ewbank et al., 2008; Herzmann, Schweinberger, Sommer, & Jentzsch, 2004; Schweinberger, Pickering, Burton, & Kaufmann, 2002; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). Hence, the viewpoint-tuning function of the N170 for individual face coding is unclear. The second goal of the present study was thus to address this question of the sensitivity of the N170 to individual faces across viewpoint changes by manipulating the identity of the face ('same' or 'different') between the adapter and the target.

Here, in order to test the viewpoint-dependence of early face representations with or without changes of identity, we used a parametric design by manipulating the head orientation of faces along a continuum ranging from 0° to 90° depth rotation, by angles of 15° (Fig. 1). An ERP face adaptation paradigm (Kovacs et al., 2006) was used during which a first (adapting, full-frontal) face was presented for several seconds (~2800 ms), followed quickly by a second one (target) presented for ~200 ms. The target face varied in terms of angle of rotation in depth (0–90°, variations of 15° angles) and identity (same vs. different). Participants performed an identity matching task between the adapting and target faces, and the analyses focused on the N170. A subsequent response elicited by the repetition of unfamiliar faces the so-called N250r ("r" for repetition effect, Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002) was also measured. This experiment was preceded by a pilot study with a small group of participants to ensure that, independently of any adaptation context, there were no differences in terms of N170 amplitude for face stimuli of different head orientations.

2. Experimental procedures

2.1. Participants

Eighteen paid volunteers (13 females, one left-handed, mean age = 20.85 ± 3.44 years) were included in the main study. Six other participants (four females, all right-handed, mean age = 22.83 ± 3.76 years) took parts in a pilot study. All participants had normal (self-reported) or corrected vision. Written informed consent was obtained from all participants prior to the experiment.

2.2. Stimuli

Thirty-two unfamiliar face identities (16 females) without glasses, facial hair or make-up, and with neutral expression were used. These stimuli were photographs of people obtained from a large database used in a previous study (Laguesse, Dormal, Biervoye, Kuefner, & Rossion, 2012). Each face was presented at 13 different angles of head rotation: six right-sided views (15°, 30°, 45°, 60°, 75°, 90°), one frontal view (0°), and six left-sided views (15°, 30°, 45°, 60°, 75°, 90°) (Fig. 1A). All face pictures were cropped to remove background, clothing and external features (including hair) using Adobe® Photoshop® 7.0. The resulting cropped faces were equated for mean pixel luminance across all conditions (average luminance = 25.3 cd/m^2) and they were also equated in size (height) using Matlab 7.0. Four hundred and sixteen face photographs were used in total (32 face identities × 13 different viewing angles).

2.3. Procedure

After electrode-cap placement, participants were seated in a light- and sound-attenuated room, at 100 cm from the computer monitor. Stimuli were displayed using E-prime 1.1, on a light gray background. In each trial, two face stimuli (adapting and target faces) were presented sequentially.

2.3.1. Pilot study

Previous ERP studies did not report N170 differences between frontal and profile views of faces (Eimer, 2000; Miyakoshi, Kanayama, Nomura, Lidaka, & Ohira, 2008). However, in order to ensure that without face adaptation there were no differences between the different head orientations used in the present study, we carried out a pilot experiment ($n = 6$ participants) in which the entire set of faces with different head orientations was presented during an independent gender discrimination task. As illustrated in Fig. 2, without adaptation, the N170 did not differ across conditions. Analyses performed on the N170 amplitude at the same three pairs of occipito-temporal (POO9/10h, PO9/10, and PPO9/10h) electrodes as those used in the main experiment revealed no significant effect of *Viewpoint* ($F(6, 30) = 1.13$, $\varepsilon = 0.37$, $p = 0.37$, $\eta p2 = 1.84$) or significant interactions involving this factor (*Viewpoint* × *Hemisphere*: $F(6, 30) = 0.29$, $\varepsilon = 0.25$, $p = 0.69$, $\eta p2 = 0.06$; *Viewpoint* × *Electrode*: $F(12, 60) = 2.1$, $\varepsilon = 0.22$, $p = 0.15$, $\eta p2 = 0.3$). However, analyses performed on the preceding P1 component for the same pairs of electrodes showed a significant interaction between *Viewpoint* and *Electrodes* ($F(12, 60) = 4.5$, $\varepsilon = 0.14$, $p = 0.05$, $\eta p2 = 0.47$) indicating an effect of *Viewpoint* in one pair of electrodes, POO9/10h ($F(6, 30) = 2.6$, $\varepsilon = 0.3$, $p = 0.47$, $\eta p2 = 0.34$). This last effect is probably due to small low-level differences between different views, which have a different surface on the screen (e.g. a 90° face has a smaller surface than a full front face, see Fig. 1A). This is because, as mentioned above in Section 2.2, face pictures were equated in size (height) but not in width in order to avoid distortion of the overall face configuration. Statistical analyses performed on the width of the pictures across the different views revealed a significant effect of *Head orientation* ($p < 0.0001$) accounted for by smaller width for 90° views compared to all other views (mean width for 90° views: 166 mm and for 0° views: 184 mm).

2.3.2. Main experiment

In the main experiment, the adapting face was presented at a full front view, and the target face was presented either also at a full front view or at rotated head views until 90° to the left or to the right side, by steps of 15°. The adapting face was always presented at full front orientation in all conditions, so that participants could not anticipate the head orientation of the target face after seeing the adapting face (Fig. 1B).

A trial started with a fixation point displayed at the center of the screen for 100 ms. Approximately 225 ms (randomized between 150 and 300 ms) after the offset of the fixation point, the adapting face appeared for ~2800 ms (randomized between 2600 and 3000 ms). After another interval of about 225 ms (150–300 ms), the target face appeared for about 200 ms (randomized between 150 and 250 ms). The target face was presented briefly so that participants had time to make only one gaze fixation on the face stimulus. Moreover, it varied in duration to minimize the contamination of late (e.g., N250r) responses by visual ERPs elicited by the offset of the stimulus. The offset of the second face was followed by an inter-trial interval of about 1400 ms (1300–1500 ms) (Fig. 1B).

In half of the trials, the target face was of the same identity as the adapting face. Each face appeared equally often in the "same" and "different" identity conditions. When the identity of the faces in a pair was different, the faces were always of the same gender. Further, when the pairs of faces were of the same identity and

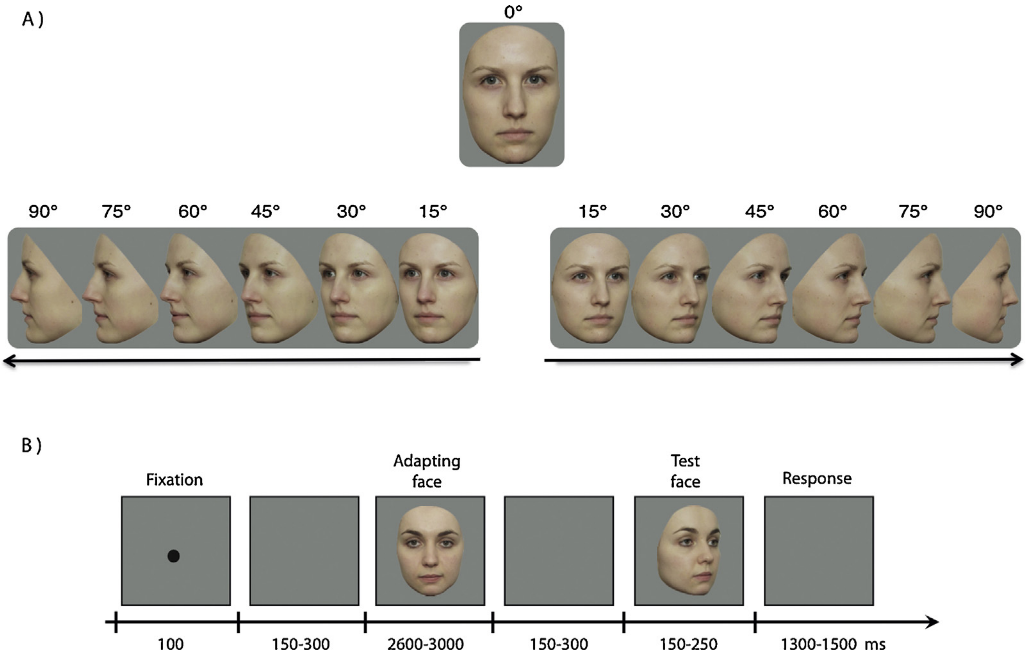

Fig. 1. (A) Examples of face stimuli at 13 degrees of head orientation, from 0° to 90° in the right and in the left side. (B) Timeline of the stimulus presentation.

presented both in a frontal view, different pictures of the same identity were used. In addition, to minimize any ERP effects due to adaptation to low-level visual features, the target face of each trial was 8% larger than the adapting face. The adapting face subtended approximately 3.3° × 4.8° of visual angle, and the target face subtended approximately 3.5° × 5.2° of visual angle.

Participants performed an individual face matching task between the adapting and target faces ("same or "different"), and gave their response by pressing one of two keys with their right hand. Response keys were counterbalanced across participants, who were instructed to maintain eye gaze fixation at the center of the screen during the whole trial and to respond as accurately and as fast as possible. Participants performed 64 trials per condition (32 faces repeated two times each, one time for head orientations to the left and the second time for head orientations to the right, in all conditions, in a 2 × 7 factorial design: *Identity repetition* (same versus different) × *Degree of rotation* (0°, 15°, 30°, 45°, 60°, 75°, 90°)). The order of conditions was randomized within each block (16 blocks of 56 trials, 896 trials in total).

2.4. EEG recording

EEG was recorded from 128 Ag/AgCl electrodes mounted in an electrode cap (Waveguard, ANT, Inc; 2D map of all electrode positions can be accessed here: http://www.ant-neuro.com/products/waveguard/electrode-layouts). Electrode positions included the standard 10–20 system locations and additional intermediate positions. Vertical and horizontal eye movements were monitored using four additional electrodes placed on the outer canthus of each eye and in the inferior and superior areas of the right orbit. During EEG recording, all electrodes were referenced online to a common average reference, and electrode impedances were kept below 10 kΩ. EEG was digitalized at a 1000 Hz sampling rate and a digital anti-aliasing filter of 0.27*sampling rate was applied at recording (at 1000 Hz sampling rate, the usable bandwidth is 0 to ~270 Hz). Electroencephalography (EEG) data were analyzed using ASA 4.6 (ANT, Inc.), and custom-made routines in Matlab 7.0. After a 0.1 Hz high-pass and 30 Hz low-pass filtering of the EEG (Butterworth filters, attenuation slope of 24db/octave), trials contaminated with eye movements or other artifacts ($\geq \pm 80\ \mu V$ in −100 to 900 ms) were marked and rejected. When there were many eye-blink artifacts, a correction was applied using a principal component analyses method (Ille, Berg, & Scherg, 2002). Incorrect trials and trials containing EEG artifacts were removed. For each participant, averaged epochs ranging from −100 to 900 ms relative to the onset of the stimulus and containing no EEG artifact were computed for each condition separately and baseline corrected using the 100 ms pre-stimulus time window. Participants' averages were then grand-averaged for data display of waveforms and topographical maps. The mean number of trials remaining after EEG processing for all conditions confounded was of 44 ± 3 trials (0°: 48; 15°: 46; 30°: 46; 45°: 43; 60°: 43; 75°: 40; 90°: 40 trials). Given these small variations between conditions, amplitude values were computed as the average value around the peak, a measure that is independent of small variations of SNR between conditions (Luck, 2005).

2.5. Statistical analyses

2.5.1. Behavior

Correct response times and percentages of correct responses were computed for each of the 14 experimental conditions for each participant and were submitted to a repeated-measures analysis of variances (ANOVA) with *Viewpoint* (0°, 15°, 30°, 45°, 60°, 75°, 90°) as within-subject factor.

2.5.2. Electrophysiology

The analysis focused on the N170 component (maximal at 170 ms on average) and the N250r (maximal at 270 ms on average). Amplitudes of the N170 was measured at 3 (PO9/10, PPO9/10h, POO9/10h) different pairs of occipito-temporal electrodes in the left and the right hemisphere where the N170 the most prominent. The electrophysiological data were analyzed from the mean amplitudes of the N170. To do that, the peak latency of the N170 on the grand averaged data was extracted automatically for each condition. Based on the values obtained, amplitudes were quantified for each condition as the mean voltage measured within 30 ms windows centered on the grand average peak latency of the N170 (i.e., 168 ms in the present study) at the three pairs of occipito-temporal electrodes. The mean amplitude of the N250r was measured in the interval from 250 to 290 ms after stimulus onset at 3 (PO9/10, P9/10, and TPP9/10h) pairs of occipito-temporal electrodes in the left and the right hemisphere where this component was the most prominent.

A complementary analysis was also performed on the preceding low-level P1 component as well on peak-to-peak N170-P1 amplitudes by subtracting the mean amplitude values of the P1 from the N170 amplitude, the P1 (110 ms peak latency) being measured at the same channels as the N170, within 30 ms windows.

The amplitude values were then submitted to separate repeated-measures analysis of variance (ANOVA) with *Identity repetition* (different vs. same identities), *Viewpoint* (0°, 15°, 30°, 45°, 60°, 75°, 90°), *Hemisphere* (right vs. left) and *Electrodes* (three levels) as within-subject factors. Since the factor "side of face rotation" (left or right) did not yield significant results, this factor was not included in the analyses. For each viewpoint, right- and left-sided views were thus merged. All effects with two or more degrees of freedom were adjusted for violations of sphericity according to the Greenhouse–Geisser correction. Polynomial contrasts were performed for post hoc comparisons. Post hoc Fisher's least significant difference (LSD) tests were used to compare the conditions two-by-two.

3. Results

3.1. Behavioral data

Participants performed the face identity-matching task with an average performance across conditions of 88%. However, performance varied as a function of *Viewpoint* ($F(6, 102) = 57.4$; $\varepsilon = 0.64$, $p < 0.0001$, $\eta p2 = 0.77$,). This effect is explained by a progressive

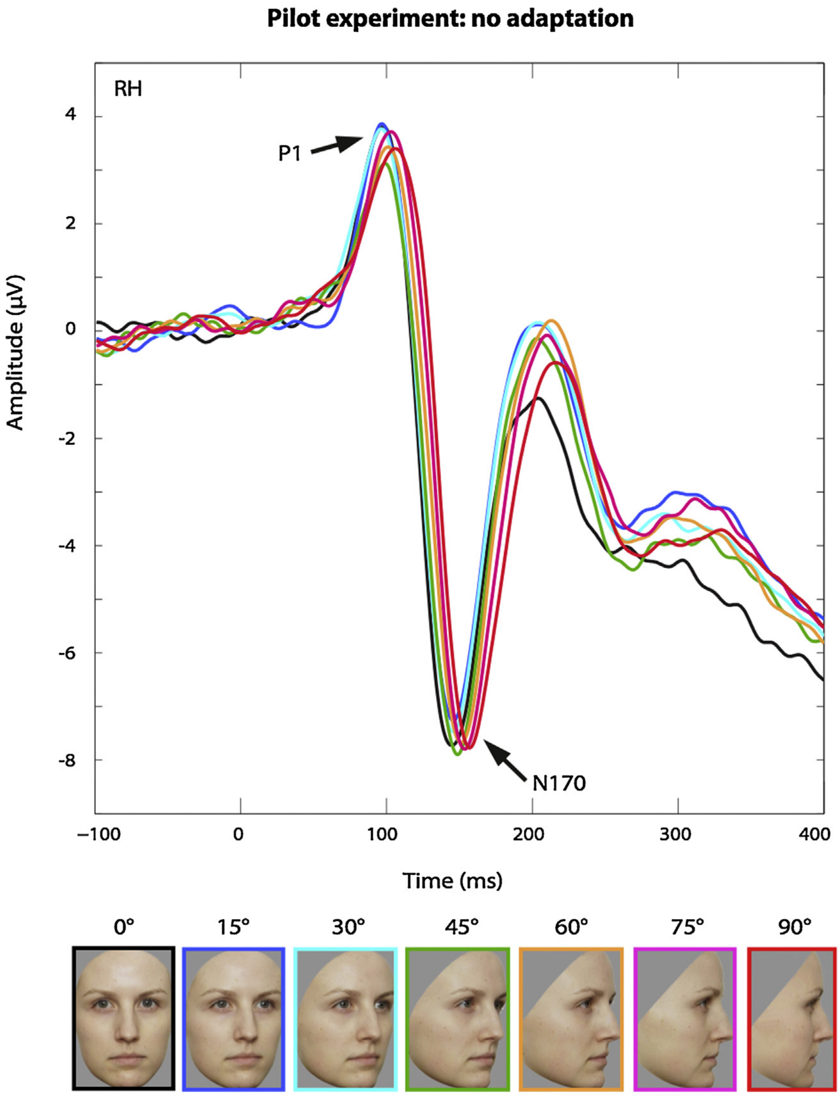

Fig. 2. Pilot study. Grand average ERP waveforms ($n = 6$ participants) (from −100 to 400 ms relative to stimulus onset) elicited by all seven viewpoints at right pooled occipito-temporal electrode sites (waveforms averaged for electrodes PO10, PPO10h and POO10h) where the P1 and N170 components peaked maximally. For each viewpoint, right- and left-sided views were merged.

decrease in accuracy when head orientation changed from 0° to 90° (Fig. 3). For accuracy rates, polynomial contrasts revealed a highly significant linear ($F(1, 17) = 146.7$, $p < 0.0001$) contrast, indicating a strong linear relationship between the increasing difference in head orientation between the adapter and the target face and subjects' performance (Fig. 3). For correct response times, the effect of *Viewpoint* ($F(6, 102) = 41.96$; $\varepsilon = 0.61$ $p < 0.0001$, $\eta p2 = 0.71$,) was also significant, an effect due to a gradual increase in response times

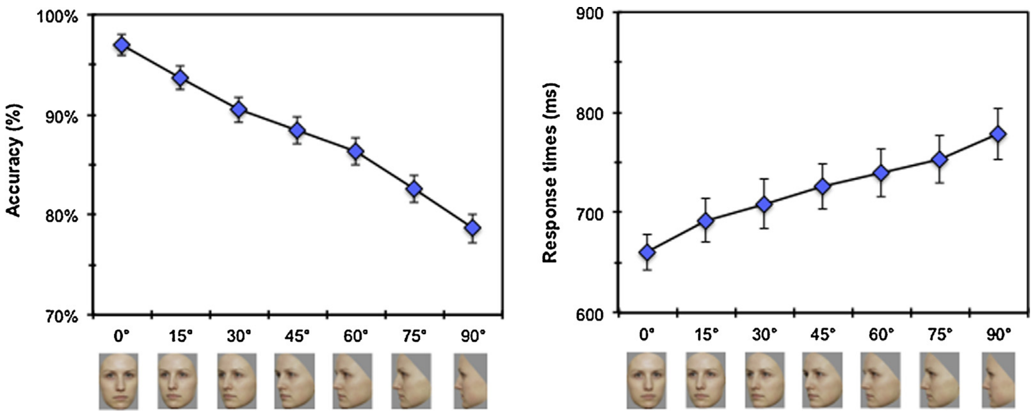

Fig. 3. Behavioral results. Accuracy in percent of correct responses and response times (±standard error) as a function of viewpoint changes.

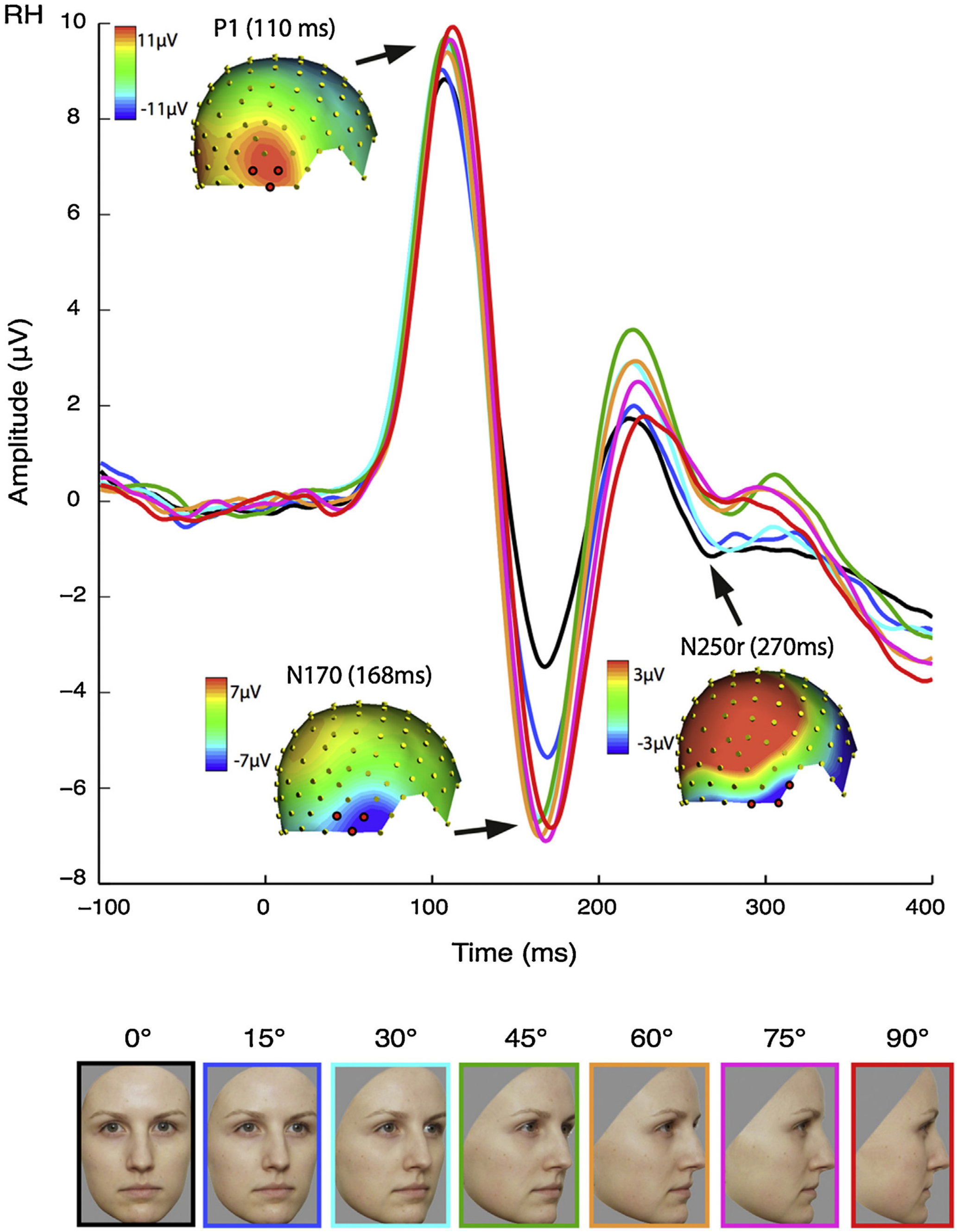

Fig. 4. Grand average ERP waveforms (from −100 to 400 ms relative to stimulus onset) elicited by all seven viewpoints at right pooled occipito-temporal electrode sites (waveforms averaged for electrodes (PO10, PPO10h, POO10h) represented in a red circle on the topographical maps resulting of an average of all the conditions) where the P1 and N170 components peaked maximally. For each viewpoint, right- and left-sided views were merged.

when head orientation increased from 0° to 90° (Fig. 3). This effect was reflected by polynomial contrasts showing a highly significant linear contrast ($F(1, 17) = 28.3$, $p < 0.0001$).

3.2. Electrophysiological data

Electrophysiological data time-locked to the presentation of the target face stimulus in an adaptation paradigm showed the classical succession of visual event-related (ERP) potentials: P1, N170 and N250r components (Fig. 4). Our hypotheses concerned the N170 component, which is the earliest high-level face-sensitive component (Rossion & Caharel, 2011), also associated with the activation of individual face representations (Rossion & Jacques, 2011). Hence, we report observations on this component primarily before reporting complementary analyses that takes into account the previous potential (P1) variations across head orientations as well as post N170 effects, i.e., the N250r component.

3.2.1. N170 component

The N170 was much larger in the right than the left hemisphere (*Hemisphere* effect: $F(1, 17) = 11.15$, $p = 0.004$, $\eta p2 = 0.4$) and there was also a significant main effect of *Electrode* ($F(2, 34) = 36.6$; $\varepsilon = 0.95$ $p < 0.0001$, $\eta p2 = 0.68$, reflecting larger N170 amplitude at PO9/10 and PPO9/10h pairs of channels). Most importantly, the N170 amplitude varied substantially as a function of *Viewpoint* changes ($F(6, 102) = 21.45$; $\varepsilon = 0.32$, $p < 0.0001$, $\eta p2 = 0.56$) (with a

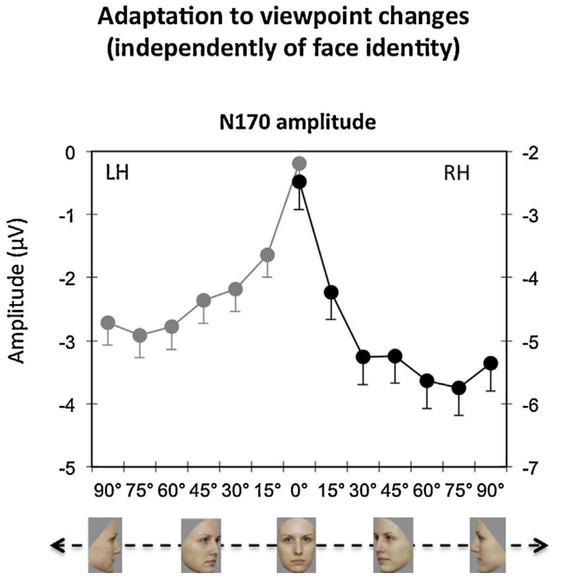

Fig. 5. Mean amplitudes of the N170 component (measured at three pairs of occipito-temporal electrodes in the left and in the right hemisphere where this component is the most prominent) as a function of face viewpoint but independently of the face identity repetition.

smaller effect of this factor on the POO9/10h electrode sites, as indicated by the *Viewpoint* × *Electrode* interaction: $F(12, 204) = 3.36$; $\varepsilon = 0.25$, $p = 0.025$, $\eta p2 = 0.16$) (Fig. 4). Post hoc comparisons indicate that this effect was due to an increase of amplitude from 0° to 15° ($p < 0.001$), and from 15° compared to all other views (all $p < 0.015$), which did not differ from each other (all $p > 0.05$) (Fig. 5). According to polynomial contrasts, the relationship between head orientation and the N170 amplitude was accounted for by a linear ($F(1, 17) = 24.1$, $p = 0.0001$) component but also by other components [i.e., quadratic ($F(1, 17) = 49.2$, $p < 0.00001$), cubic ($F(1, 17) = 4.6$, $p = 0.046$), and quartic ($F(1, 17) = 5.05$, $p = 0.038$)], indicating a significant deviation from linearity.

The main *Identity repetition* effect ($F(1, 17) = 2.82$, $p = 0.1$, $\eta p2 = 0.14$) was not significant. However, critically, there was a significant *Identity repetition* × *Viewpoint* interaction ($F(6, 102) = 3.22$; $\varepsilon = 0.67$, $p = 0.017$, $\eta p2 = 0.16$). This effect was accounted for by a significant *Identity repetition* effect—i.e., larger amplitude for different identities than for same identities—for the viewpoints of 0° ($p = 0.011$), 15° ($p = 0.05$), and 30° ($p = 0.015$), but not for the other viewpoints (for 45°: $p = 0.7$; 60°: $p = 0.9$; 75°: $p = 0.4$; 90°: $p = 0.09$) (Figs. 6 and 7A). The magnitude of the Identity repetition effect did not differ among 0°, 15° and 30° ($F(2, 34) = 0.49$; $\varepsilon = 0.97$ $p = 0.61$, $\eta p2 = 0.03$). All other effects, including the three-way interaction between *Viewpoint*, *Identity repetition* and *Hemisphere*, were not significant ($p > 0.2$).

In summary, we observed an effect of viewpoint, the N170 being smaller in amplitude for no change of view and then for change of 15° between the adapting and the target faces, than for all subsequent views. The *Identity repetition* effect was significant for 0°, 15° and up to 30° and stable across these views.

3.2.2. P1 component

With respect to P1 amplitude, there was a significant *Viewpoint* effect ($F(6, 102) = 5.81$; $\varepsilon = 0.67$, $p = 0.0004$, $\eta p2 = 0.25$) reflecting smaller amplitudes for 0° and 15° (with no significant difference between these two first views: $p = 0.2$) as compared to all others view angles (all $p < 0.05$) and smaller amplitudes for 60° and 75° as compared to 90° (all $p < 0.03$) (Fig. 4). Polynomial contrasts revealed for the P1 amplitude modulations with viewpoint, significant linear ($F(1, 17) = 15.23$, $p = 0.001$), cubic ($F(1, 17) = 10.7$, $p = 0.004$) and quartic ($F(1, 17) = 5.5$, $p = 0.03$) components. Although this effect of viewpoint was significant for all pairs of electrodes, this effect was smaller at P09/10 and POO9/10h electrode sites as compared to PPO9/10h electrode sites, as revealed by a significant *Viewpoint* × *Electrode* interaction ($F(12, 204) = 3.77$; $\varepsilon = 0.38$, $p = 0.005$, $\eta p2 = 0.18$). A significant *Identity repetition* effect ($F(1, 17) = 12.71$, $p = 0.002$, $\eta p2 = 0.43$) was also observed, the P1 amplitude being larger for different face identities than for same identities (Fig. 6). However, critically the interaction between the factors *Identity repetition* and *Viewpoint* was not significant ($F(6, 102) = 0.31$, $\varepsilon = 0.59$, $p = 0.85$, $\eta p2 = 0.02$), indicating that the *Identity Repetition* effect was independent of the viewpoint changes.

In summary, there were smaller but significant effects of *Viewpoint* and *Identity Repetition* already at the level of the P1. These effects should be treated with caution because the P1 component's

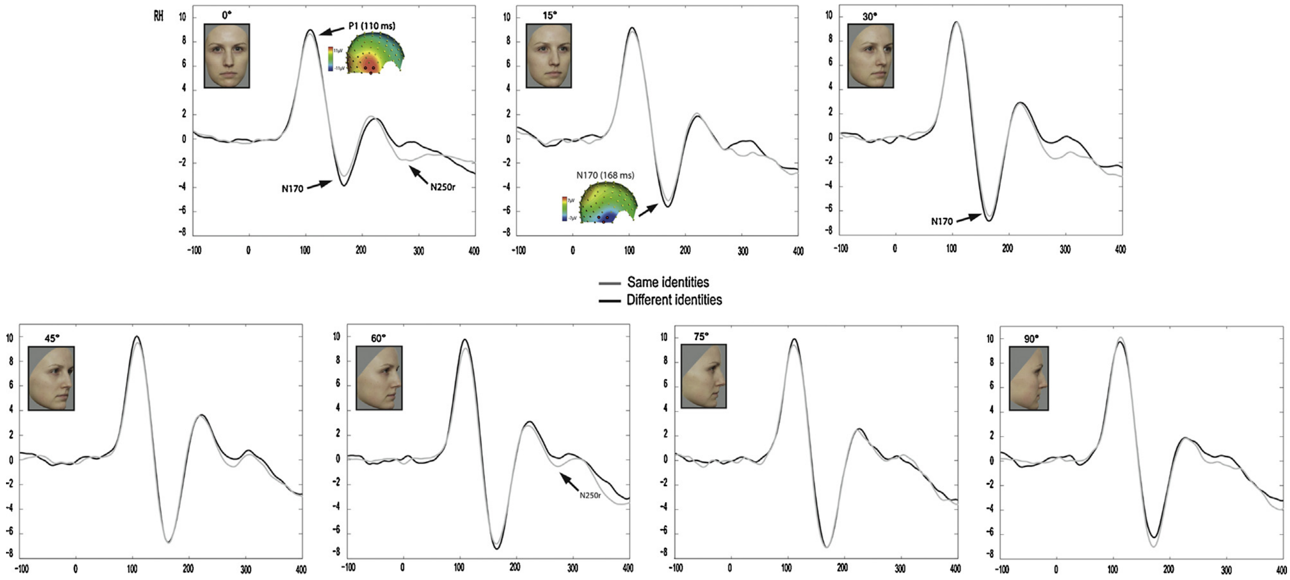

Fig. 6. Grand average ERP waveforms (from −100 to 400 ms relative to stimulus onset) at right pooled occipito-temporal electrode sites (waveforms averaged for electrodes represented in a red circle on the topographical maps resulting of an average of all the conditions: PO10, PPO10h, POO10h). ERPs are shown as a function of Viewpoint and Identity repetition (same vs. different identities).

face-sensitivity, contrary to the N170, is due to low-level cues (Rossion & Caharel, 2011), which cannot be perfectly controlled in the present experiment (e.g., variations of the surface of the stimuli for different views, see Section 2.3.1) and were partly present even without adaptation (pilot experiment, see Section 2.3.1). Therefore, to rule out that the effects observed on the component of interest, the N170, were due to small variations already present at the level of the P1, we ran a peak-to-peak analysis to complement the baseline-to-peak analysis, for the three effects of interests that were significant on the N170.

3.2.3. *Peak-to-peak (N170-P1) analyses*

The N170-P1 difference was modulated by *Viewpoint* changes ($F(6, 102) = 29.21$; $\varepsilon = 0.30$, $p < 0.00001$, $\eta p2 = 0.63$) explained by an increase in amplitude from 0° to 15° ($p < 0.00001$) and from 15° to all other head orientations (all $p < 0.0004$), which did not differ from each other (Fig. 7B). Polynomial contrasts revealed that the relationship between face viewpoint and the N170-P1 amplitude was a combination of linear ($F(1, 17) = 13.2$, $p = 0.002$), quadratic ($F(1, 17) = 30.5$, $p < 0.0001$) and cubic ($F(1, 17) = 18.0$, $p = 0.0005$) and quintic ($F(1, 17) = 5.8$, $p = 0.02$) components.

There was a significant *Identity repetition* effect ($F(1, 17) = 24.83$; $p = 0.0001$, $\eta p2 = 0.59$) due to larger amplitude for different compared to same face identities. In addition, a significant *Identity repetition* × *Viewpoint* interaction ($F(6, 102) = 2.63$; $\varepsilon = 0.71$, $p = 0.035$, $\eta p2 = 0.14$) was found, due to significant *Identity repetition* effects—i.e., larger amplitude for different identities than for same identities—for viewpoints of 0° ($p = 0.0008$), 15° ($p = 0.024$), and 30° ($p = 0.026$), but not for any of the others viewpoints (for 45°: $p = 0.2$; 60°: $p = 0.1$; 75°: $p = 0.8$; 90°: $p = 0.3$) (Fig. 7B). The magnitude of the Identity repetition effect did not differ among 0°, 15° and 30° ($F(2, 34) = 1.8$; $\varepsilon = 0.99$, $p = 0.2$, $\eta p2 = 0.09$).

In summary, although a peak-to-peak analysis between components reflecting different processes should be treated with caution, the outcome of the analysis is exactly the same as for the analysis of the N170, showing that the N170 effects of *Viewpoint* and *Identity Repetition*, as well as the interaction between these two factors, are not related at all to any small variations observed on the low-level P1 component.

3.2.4. *N250r component*

Contrary to the N170, the N250r was larger in the left than the right hemisphere, especially at lateral (TTP9/10h, P9/10) electrode site ($F(2, 34) = 25.14$, $\varepsilon = 0.86$, $p < 0.0001$, $\eta p2 = 0.6$), as indicated by the *Electrode* × *Hemisphere* interaction ($F(2, 34) = 10.06$; $\varepsilon = 0.81$, $p = 0.001$, $\eta p2 = 0.4$). The N250r amplitude was also modulated by *Viewpoint* changes ($F(6, 102) = 5.01$, $\varepsilon = 0.45$, $p = 0.005$, $\eta p2 = 0.23$) due to a decrease in amplitude with increasing head rotations. Specifically, the relationship between the N250r amplitude and face viewpoint was reflected only by a significant linear component ($F(1, 17) = 9.2$, $p = 0.007$). The two-by-two comparisons showed significant differences among viewpoints of 0°, 15°, and 30° (with no significant difference among these three viewpoints, all $p > 0.05$) with viewpoints of 45°, 60°, 75° and 90° (with only one significant difference among these four viewpoints, namely between 45° and 90°: $p = 0.03$) (Fig. 4). Furthermore, there were significant interactions between *Identity repetition* × *Viewpoint* but only on low channels TPP9/10h ($F(6, 102) = 3.6$, $\varepsilon = 0.62$, $p = 0.012$, $\eta p2 = 0.17$), and P9/10 ($F(6, 102) = 4.17$, $\varepsilon = 0.59$, $p = 0.006$, $\eta p2 = 0.2$) (as qualified by a three-way interaction between *Identity repetition* × *Viewpoint* × *Electrode*: $F(12, 204) = 2.15$, $\varepsilon = 0.54$, $p = 0.048$, $\eta p2 = 0.12$). At these electrodes, *Identity repetition* effects were observed regardless of head orientation (in both pairs of electrodes, all $p < 0.05$), the significant interaction being due to a larger repetition effect for 0° than all other viewpoints (Fig. 6).

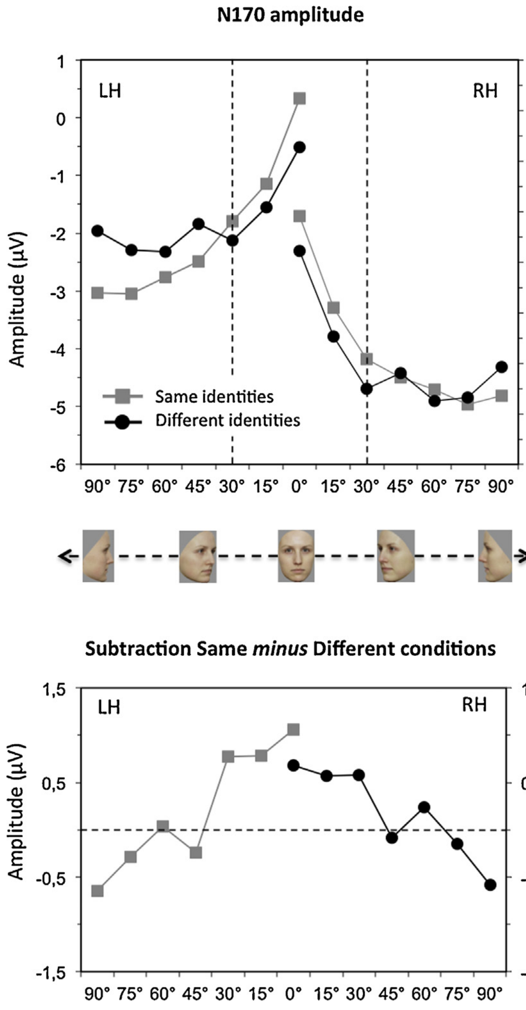

Fig. 7. Mean amplitudes of the N170 component and as a function of face viewpoint and identity repetition (same vs. different identities). These values were measured at three pairs of occipito-temporal electrodes in the left and in the right hemisphere (PO9/10, PPO9/10h, POO9/10h). The graph at the bottom represents the magnitude of identity repetition effect (same *minus* different conditions) for each viewpoint.

4. Discussion

4.1. *The N170 reflects the activation of viewpoint-dependent face representations with a gradual tuning until 30°*

The N170 marks the first activation of a face representation in the human brain: contrary to earlier responses, it is elicited by stimuli that are perceived (i.e., interpreted) as faces, independently of their physical properties (Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002; Caharel et al., 2013; Churches, Nicholls, Thiessen, Kohler, & Keage, 2014; George et al., 2005; for reviews, see Rossion, 2014; Rossion & Jacques, 2011). When there is no adaptation (Fig. 2), the N170 does not vary in amplitude between different views of faces. This observation agrees with, and extends, previous observations of no N170 differences between frontal and profile views of faces (Eimer, 2000; Miyakoshi et al., 2008). It suggests that any view of a face picture, at least when its characteristics features are still visible, triggers this initial visual representation. However, most importantly, in an ERP adaptation paradigm in which an adapting face is presented in full-front view followed by a target face varying parametrically in terms of angle of rotation (from 0° to 90° by steps of 15°), the N170 is reduced in amplitude when the target face is presented exactly at the same view as the adapter (0°) and then increases progressively in amplitude from 0° to 30° changes of viewpoint, with no further modulation between 30° until 90° rotation. This finding cannot be accounted for by small variations of the number of correct trials across conditions, since the number of trials decreased slightly after the 30° head orientation only. Similarly, these findings cannot be accounted for by an increased difficulty in matching the face views, since this increase is strictly linear from 0° to 90° head orientations. It is an important finding because it provides evidence that the earliest face representation activated in the human brain—as indexed by the N170—is viewpoint-dependent. That is, at the entry level of the face perception system, a full-front face and a 30° depth-rotated face are not encoded by the exact same populations of neurons, a conclusion that could only be reached by using an ERP face adaptation paradigm. This finding generally agrees with fMRI adaptation studies reporting that face-selective areas of the middle fusiform gyrus and of the posterior STS are sensitive to head orientation (Andrews & Ewbank, 2004; Fang et al., 2007; Grill-Spector et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, Vuilleumier, 2005a,b). The strength of viewpoint adaptation in these cortical regions, which certainly contribute to the N170 recorded on the scalp (e.g., Horovitz, Rossion, Skudlarski, & Gore, 2004; Lidaka, Matsumoto, Haneda, Okada, & Sadato, 2006; Sadeh, Podlipsky, Zhdanov, & Yovel, 2010), also depends on the angular difference between the adapting and target faces (Fang et al., 2007). However, due to the poor temporal resolution of the fMRI technique, these studies were unable to tell that the *early* representation of faces in the human brain is viewpoint-dependent, an information provided by the present observations.

Interestingly, the intermediary view between 0° and 30°, i.e., a head orientation with a 15° depth-rotation, was associated with an N170 whose amplitude was roughly in between the N170 amplitude of the 0° view and of the 30° view. This observation indicates that populations of neurons coding for the 15° head orientation view overlap partially with populations of neurons coding for the 0° view and the 30° view. This finding can be accounted for by a viewer centered tuning according to which the populations of neurons respond maximally for a given view (for instance 0° as tested here) and decrease their firing rates roughly monotonically with head rotation until 30°.

This account is in line with the findings of non-human primate single-cell recording studies indicating that face-selective neurons in the inferior temporal cortex (IT) are mainly viewpoint-dependent and show a progressive decrease in firing rate with increasing distance from their preferred head orientation (Desimone et al., 1984; Perrett et al., 1985, 1991).

However, the tuning function evidenced in the present study is rather narrow: at 30° head orientation, the N170 is as large as at 90° head orientation, suggesting a full recovery from adaptation at the 30° view (Figs. 4 and 5). This narrow tuning may be due to the use of a full front view as adapting face, and we cannot exclude that the full recovery of the N170 amplitude for a target face that differs by 30° head orientation from the adapting face would be observed with a 45° adapting face for instance (i.e., full recovery for a 15° and 75° head orientations).

4.2. *Face identity repetition resists viewpoint changes until 30°*

The second goal of the present study was to examine the viewpoint-dependence or -independence of early face representations to changes of identity. Behaviorally, we found a linear increase of error rates and RTs in matching faces across viewpoint changes, the performance decreasing by about 20% between no change of head orientation (i.e., 0° to 0°) and a 90° difference (i.e., 0° to 90°). These findings are consistent with behavioral studies showing that the size of adaptation effects drops drastically when the difference of viewpoint between an adaptor and a target face increases (Benton et al., 2006; Jiang et al., 2007), suggesting that human encoding of facial identity is based on viewpoint-dependent mechanisms (Benton et al., 2006; Fang & He, 2005; Hill et al., 1997; O'Toole et al., 1998; Troje & Bülthoff, 1996).

Here, we confirmed the now well-established evidence for an early identity repetition on the N170 for unfamiliar faces (i.e., small N170 amplitude after consecutive presentation of the same as compared to different facial identity) (Caharel, d'Arripe, et al., 2009; Caharel, Jiang, et al., 2009; Caharel et al., 2011; Ewbank et al., 2008; Harris & Nakayama, 2007; Heisz et al., 2006; Itier & Taylor, 2002; Jacques et al., 2007; Jacques & Rossion, 2009). This effect indicates that the extraction of individual face representations takes place early at around 170 ms post-stimulation. In two previous reports (Caharel, d'Arripe, et al., 2009; Caharel et al., 2011), we found that this effect was present for 30° changes of viewpoint. However, these studies did not compare conditions with or without viewpoint changes and could not compare the magnitude of this effect across viewpoint changes. Thus, the present study goes beyond these findings by providing evidence that the N170 identity adaptation effect is robust enough to generalize fully across different head orientations, up to 30°. Specifically, the N170 amplitude at occipito-temporal regions in response to the target stimulus was reduced for repeated as compared to different faces, whether there was no change of viewpoint, or changes of 15° and 30° between the adapting and the target faces. Moreover, contrary to our previous observations, at least for unfamiliar faces, this effect was found at both the left and right hemispheres in the present study, perhaps because the initial stimulus was a full front face rather than a stimulus rotated to the right. This generalization across views for the coding of face identity is in agreement with fMRI studies, which reported some degree of generalization across views in the ventral occipito-temporal cortex (Anzellotti, Fairhall, & Caramazza, 2013; Pourtois et al., 2005a), but again without being able to determine whether this effect emerges as early as the first activation of individual face representations.

Interestingly, beyond a change of 30° between the two faces, the identity adaptation effect disappeared entirely. Thus, the partial transfer of this early (N170) face identity repetition across viewpoint changes indicates that individual face representations activated during the N170 time-window generalize across views, unless the disparity in head rotation is too important (i.e., 45° or more). One potential reason for this lack of transfer across large head orientation disparities may be that the internal facial features (eyes/eyebrows, nose, mouth) are no longer visible in a 45° face (Fig. 1)

In line with previous reports (Begleiter, Porjesz, & Wang, 1995; Caharel, d'Arripe, et al., 2009; Caharel et al., 2011; Gosling & Eimer, 2011; Herzmann et al., 2004; Jacques et al., 2007; Schweinberger et al., 1995; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002), we also found later effects of (unfamiliar) face identity repetition at around 250 ms following stimulus onset, reflected by more negative amplitude of the N250r for repeated as compared to unrepeated faces. This finding has been related to the activation of memory representations of individual faces (Herzmann et al., 2004; Schweinberger et al., 1995; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002). Interestingly, thanks to the parametric manipulation used in the present study, we found that this identity repetition effect is preserved irrespective of viewpoint changes, even though the magnitude of this effect was the largest when there was no change of viewpoint between the repeated faces. Thus, even if the N250r shows a certain degree of image specificity (Schweinberger, Pickering, Jentzsch, et al., 2002), these observations provide evidence that, at this relatively late time point of processing, representations of individual unfamiliar face have become more viewpoint-independent (invariant), an effect which may emerge after the same individual face has been encountered repeatedly (Zimmermann & Eimer, 2013).

5. Conclusions

To summarize, the first main finding of the present study is that face representations activated as early as 170 ms after stimulus onset in the occipito-temporal cortex are viewpoint-dependent: partially different populations of neurons encode different views of faces, at least for a 0° and 30° head orientations. The second main finding is that the representation of face identity activated during the N170 temporal window generalizes fully across viewpoint changes, unless the disparity in head orientation is too large (45°). At a later time point of face processing, at around 250 ms, sufficient information has accumulated in the human brain so that individual face representations become more viewpoint-independent (invariant).

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